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BY

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SYNOPSIS

The paper discusses the environmental conditions prevailing in the Lower Lias of England with particular reference to the insect faunas contained in the sediments. It also discusses the degree of salinity insects can withstand. The environment of the Lias is compared with that of the Bombay coast of today, with its numerous islands and inlets, and mud sedimentation.

The new fauna from Charmouth, with six dragonflies, one orthopteron and three beetles, is described. The dragonflies all belong to the almost extinct Anisozygoptera and are among the largest known. The orthopteron belongs to the almost extinct Prophalangopsidae, being their most primitive representative and linking them with the Gryllacrididae. Of the beetles, one is a Cupedid, a member of a family that flourished in the late Palaeozoic ; the two others are of unknown affinities. The structure and coloration of the elytra are analysed and interpreted in detail, providing information about the process of fossilization. The taxonomic status of the two species of *Holcoëlytrum* is discussed and types are designated.

1. GENERAL PALAEOBIOLOGICAL CONSIDERATIONS

An important collection of fossil insects has recently been made by Mr. J. F. Jackson from the " Flatstones " and related deposits near Stonebarrow, Charmouth, on the Dorset coast. The preliminary classification of the specimens, which have been acquired by the British Museum (Natural History), has shown that both in the composition of the fauna and in the preservation they resemble those of the Lower Lias of Gloucestershire, Warwickshire and Worcestershire, though there are some significant differences. Conditions of life, death and fossilization were evidently somewhat similar. In detail, however, several problems arise when the faunal association is studied. Some insects, for instance, including a dragonfly (In. 49573), rest directly on or are closely associated with ammonites.

According to Mr. Jackson (written communication) the following ammonites occur in the deposit : *Asteroceras obtusum*, *Xipheroceras dudressieri*, *Xipheroceras* sp., *Promicroceras planicosta*, very abundant. Fishes are present also and, according to Mr. Jackson's observations, mostly found where plant remains occur. The following species have been recorded : *Dapedium granulatum*, *Dapedium* sp., *Pholidophorus* sp. and *Chondrosteus* sp. (very rare).

Lamellibranchs are rare, except *Inoceramus*, and gastropods are absent. Plants, apart from driftwood, are also rare.

This list of fossils indicates salt-water, with tolerable living conditions in the water itself, whilst conditions on the sea-floor appear to have been unsuitable for many groups one might normally expect to be present. The environment would thus have been essentially marine, and there is a contradiction in the presence of numerous insects together with a marine fauna. The first possibility requiring consideration is that sea-water was less saline in Jurassic times than it is at the present day. An assessment can be made with the aid of Conway's important paper

(1943). From his data it can be calculated that the salinity of the Jurassic ocean was of the order of 3·0%,[1] in other words only slightly less than the ocean of the present (3·4%).

Since British Liassic insect faunas contain fair numbers of species which pass their larval lives in water, the resistance of insects to sea-water needs consideration. Some Apterygota are able to stand temporary submergence and to float on the water of rock pools which are their ordinary environment. A collembolon, *Lipura maritima* L., lives on the shores of Britain ; it is frequent for instance at Selsey in Hampshire on the quiet surface of pools. Another species of the same order, *Actaletes neptuni* Giard, lives on the coast of France where it is temporarily submerged by the tide. But since Apterygota have not yet been recorded from the British Lias, these forms merely indicate possibilities of adaptation. Of greater interest are certain species of Diptera, the larvae of which live on decaying organic matter in jetsam accumulations. They withstand frequent wetting and temporary submergence. A few Diptera are known from the Lias,but nothing is known about their larval modes of life.

There are, however, two important groups with aquatic larvae, the adults of which are well represented in the British Lias, the dragonflies (Odonata) and the caddisflies (Trichoptera). Both are known to occur in brackish water, and their presence in the Baltic Sea has received some attention.

Leander (1901) gave a list of the insects occurring in the sea-water west of Helsinki, Finland. He quoted twenty-one species, comprising one mayfly, nine caddisflies, two bugs, three mosquitoes (two *Chironomus*, one *Ceratopogon*) and six water beetles. These species were found among the islands and associated with the jelly-fish, *Aurelia aurita*, the worm, *Nereis diversicolor*, the barnacle, *Balanus improvisus*, the bivalve, *Cardium edule*, and others. This mixture of freshwater insects and marine species exists in water with about 0·5% of salt.

Silfvenius (1905) reported on the caddisflies found at the entrance of the Finnish Gulf at Tvärminne. The water contains 0·5–0·6% of salt, and no fewer than twenty-four species of caddisflies live in it as larvae, six of them being abundant. It is noteworthy that the bladder-wrack, *Fucus* sp., serves both as food for the larvae and as building material for their cases.

Ussing (1918) studied the insects of the Randers Fjord in Denmark, in which the concentration of salt decreases inland. He found the following :

Salt content	Insects present
Surface 1·7% Depth 2·4%	*Chironomus* larvae only.
Surface 1·2% Depth 1·9%	One dragonfly, 1 water bug, 4 water beetles, 1 leaf beetle, *Chironomus*.
Surface 0·5% Depth 1·3%	Two caddisflies, 1 dragonfly, 1 bug, 4 water beetles, 2 leaf beetles, *Chironomus*, 1 moth.
Surface 0·14% Depth 0·16%	Insect life abundant.

[1] Almost the same value is obtained, whether the calculation is based on sodium or on the total of chlorides.

This evidence shows that insect life does not altogether shun salt water, although at concentrations over 0·2% very few species are able to exist, chief among them dragonflies, caddisflies and *Chironomus* mosquitoes. Only the caddisflies, however, have gone some way towards adapting themselves to this environment, as shown by the use of *Fucus* as food as well as building material.

The Recent examples given can be supplemented by a Miocene locality (Zeuner, 1938), the *Hydrobia* Limestone of the Mayence Basin. The brackish character of the water may here be suspected, though not proved, by the abundance of the gastropod *Hydrobia* sp.[1]. The analysis of the insect fauna presents the following picture :

Terrestrial and flying individuals .	139
Aquatic individuals . . .	More than 8

The aquatic individuals comprise two adult water beetles and larvae of Hydrophilidae, two larvae of dragonflies, and larvae of Diptera (Stratiomyidae). Though the larvae have not all been studied, their total will remain small. This particular fauna, from Mombach, differs, in the scarcity of aquatic larvae, from neighbouring localities in which whole beds are composed of the cases of caddisfly larvae. Locally, therefore, and at certain times, the water was inhabited by enormous numbers of these insects. Even at Mombach, however, where no caddis cases have been found, adult caddisflies comprise 50% of the fauna. Adding to these the dragonflies, being aquatic as larvae, and the larvae of the Hydrophilidae and Stratiomyidae, the total of insects dependent on water rises to 63%. This composition suggests that at Mombach the water itself was only partially inhabitable, and this for certain insects only, whilst at other places in the neighbourhood the water must have harboured an abundance of insect larvae. It suggests that the salinity of the lake in which the *Hydrobia* Limestone formed was near the upper limit of concentration bearable by insects, and that in the immediate vicinity enough fresh water, possibly from springs, was available. Such diversity of local biotopes, not evident from the study of the embedding sediment, is by no means exceptional.

On the shore of the Dead Sea in Jordan, for example, a few freshwater pools are fed by springs, as at 'Ain Feshka. They support fishes (*Cyprinodon sophiae, C. cypris, C. dispar*). Only about 10 ft. of beach gravel separates these fishes from the deadly brine of the sea, and on this beach the writer found dead water beetles and locusts. If this combination of species occurred in a fossil context, one would almost certainly credit the Dead Sea with a fish fauna, with insects living in its water as larvae, and with other insects living in the neighbourhood. It is this complexity of the local biotopes that makes the environmental interpretation of fossil insect faunas somewhat difficult. The identification of groups with special environmental requirements and the relative frequency of individuals in the various environmental groups is, however, of considerable use as shown by the examples here quoted.

The Liassic deposits of the south-western Midlands have yielded a fauna which may be regarded as representative of woodlands interrupted by water readily in-

[1] The Oligocene of the Rhine Rift is rich in salt deposits, and the partly saline character of the *Hydrobia* Limestone was first suggested by Wenz (1921), though he was not using evidence based on insects.

habitable by insects. Dense vegetation on the water's edge is suggested. The presence of water of a salinity approaching that of the sea cannot be excluded, but there must have been plenty of accumulations of water less saline than 0·2%, to enable the abundant fauna of caddisflies, dragonflies and others to rear their larvae. The presence of humid ground is indicated by a group of crickets which appears to be related to *Pteronemobius*, and which burrows in moist ground near puddles of water under the surface. Many other Orthoptera Saltatoria are conspicuous in this fauna, the Prophalangopsidae being an almost exclusively Jurassic family which appears to have been living among leafy vegetation. The Panorpoid Complex is well represented, apart from caddisflies, by the Orthophlebiidae, the larval environment of which is unfortunately not yet known.

Turning now to the insect fauna of the Charmouth Lias, of which 434 specimens are known, it is noteworthy that no aquatic larvae have so far been discovered. Adult caddisflies, too, are completely absent. Among the remainder, the beetles (38·1%) and the Saltatoria (20·8%) dominate. Other groups are represented in small numbers only. These are the Panorpoid Complex (3·2%), Odonata (2·5), Rhynchota (2·5%) and Blattodea (1·8%). 31·1% cannot be classified without further detailed work, and many of these are too poorly preserved to be of interest. If one compares this list with the brackish faunas quoted above, it becomes clear that the insects of Charmouth are at least predominantly derived from another environment, and that their life cycles were not dependent on the water in which they were embedded and which, presumably, was too saline.

Furthermore, the numerical distribution of insect groups in the Charmouth fauna is clearly a function of their resistance to mechanical disintegration. This is why beetles are conspicuous. With them must be ranked the bugs which have hard bodies and, to a lesser extent, the cockroaches. Wings of dragonflies also are resistant to decay in water, and, unlike specimens from the Lias of the Midlands, no bodies have been bound.

The fragile forms belong to the grasshoppers and to the Panorpoid Complex. The former are often very poorly preserved; many wings are folded over as if by a changing water current. But there are a number of legs, and a few specimens appear to be almost complete with body. This group, therefore, is rather better preserved than the remainder. Apart from the single specimen of *Protohagla langi* sp.n., which is a Prophalangopsid, the great majority of other Saltatoria (if not all) belong to the Elcanidae. This well-known Jurassic family had enlarged spines on the hind tibiae with which it was able to swim, the body being held on the water by surface tension and cutaneous fat, whilst the hind tibiae were dipped into the water, serving as oars.[1] The Elcanidae, which are the ancestors of the Tertiary and Recent Tridactylidae which live on the edge of water and are likewise able to swim, were relatively fragile insects. Their abundance implies that the shore was not far away, and that the surface was not often disturbed by wave action. Salt water would not have affected them.

The Panorpoid Complex from Charmouth contains several groups, Neuroptera, Mecoptera (of which *Orthophlebia* is represented) and Diptera. In addition, there is

[1] First noted by Handlirsch (1908), phylogenetic relations discussed by Zeuner (1938).

a solitary Hymenopteron of the sawfly type. All these are poorly preserved, and their number may increase as the undetermined remainder is studied. They provide further evidence that the Charmouth insects had undergone transport and decay before they were embedded in the sediment.

Whilst this is obvious even from the condition of many Elcanidae, the more resistant beetles bear it out in an interesting manner. There are many isolated elytra, though bodies, with or without elytra, are not rare. Legs and other appendages are lost without exception. The condition of the Coleoptera is in this respect reminiscent of those found in present-day jetsam, in which they dry out periodically, acquire some buoyancy and are thus washed away and re-deposited several times. Jetsam sedimentation of insects has been described by Trusheim (1929), Schwarz (1939) and Zeuner (1938 : 151). These authors agree that off-land winds play an important part in such formations.

In the Charmouth Lias, jetsam is not likely to have been the cause of the presence of insects. If so, there should be evidence in the form of belts of concentrated fragments of vegetation mixed with marine forms as well as insects. The state of preservation of the present material does not support this idea.

Since the sediment must have been a calcareous mud deposited near land, the possibility of direct wind transport of insects on to wet mud-flats at low tide has to be mentioned. It was so in the case of the Solnhofen Limestone of Upper Jurassic age (Abel, 1929 ; Zeuner, 1939 : 20). Under such conditions, whole insects are often blown on to the flats, where they remain stuck, unable to rise again. They are thus not infrequently embedded in positions indicating their struggle to free themselves. That this interpretation does not apply to the Charmouth Lias is evident.

There remains the possibility of flotsam, of prolonged drifting and slow sinking, followed by incorporation in soft calcareous and bituminous mud, under either tidal or non-tidal conditions. Drifting is partly suggested by the fragmentary condition of most of the insects, though this may be due to other causes such as attack by predators. There is, however, conclusive evidence for extreme water-logging. Several of the beetles are compressed dorsoventrally, which is possible only when they were softened by prolonged wetting and decay. Elytra are often flattened, though by no means always, and they show wrinkles which were produced as the flattening proceeded under the weight of the freshly forming sediment. Furthermore, the wing of *Petrophlebia anglicanopsis*, a dragonfly to be described later in this paper, has its margin characteristically frayed as in modern insect wings that have begun to decompose in water.

These observations favour the interpretation of the insects as flotsam, as indeed does the composition of the fauna. The same can be applied to the Midlands Lias, but there the percentage of fragile insects is so much higher, and the abundance of caddisflies so suggestive of less saline conditions that the environment cannot have been precisely the same.

In the light of the evidence cited from other localities and of the observations made on the material from the Midlands Lias and that of Charmouth respectively, the following deductions may be made concerning the environment. In both areas, mud sedimentation occurred under protected conditions and proceeded in the virtual absence of wave action. The marine fauna may be regarded as implying that tides were present, and there are plenty of present-day areas of sedimentation that fulfil these conditions, especially on the mangrove coasts of the tropics. Those known to the writer are on the coast of Bombay and the Gulf of Cambay. The coast north of Bombay is particularly suitable for comparison. There are numerous low islands which, going inland, fuse into strips of land interrupted by numerous water inlets of varying width. These, in turn, link up with rivers which reduce the salinity of the water until, some 20 miles inland, it is fresh. Mud sedimentation under quiet tidal conditions can be observed in many places. Where tested, the mud is both calcareous and rich in organic matter. Dense vegetation on the islands and the shores harbours a rich fauna of insects, and marine species penetrate as far inland as decreasing salinity will permit them to go. In such an area, one would place the Charmouth Lias among the islands near the open sea, and the Midlands localities within the inlets.

The complete description of the fauna from Charmouth will require considerable time, partly because the poor state of preservation imposes a heavy strain on the eyes of the investigator, and partly because the fragments require large-scale comparison with more complete material from a great variety of insect orders. In this first descriptive part, all the remains of Odonata are described and referred to six species, three of which are new. In addition, the new Prophalangopsid orthopteron is described because of its phylogenetic interest, together with three species of beetles.

2. SYSTEMATIC DESCRIPTIONS

Order *ODONATA*

Suborder ANISOZYGOPTERA Handlirsch

DIAGNOSIS. Nodus placed at great distance from the base of the wing.

DISTRIBUTION. Mainly Jurassic, with two Recent species.

Family LIASSOPHLEBIIDAE Tillyard

EMENDED DIAGNOSIS. Tillyard's definition (1925 : 11) has now to be modified in so far as the discoidal cell of the fore wing is sometimes closed basally.

DISTRIBUTION. So far known from the British Lias only, with two genera containing nine species (including those here described for the first time).

Genus ***PETROPHLEBIA*** Tillyard (1925 : 11)

TYPE SPECIES. *Petrophlebia anglicana* Tillyard.

Petrophlebia anglicanopsis sp. n.

(Pl. 24, figs. 1, 2)

DIAGNOSIS. Hind wing with CuA_2 less curved than in the type species, and with indistinct distal portion.

MATERIAL. The holotype, British Museum (Nat. Hist.) In. 49573, Jackson Coll., (Pl. 24, fig. 1) with counterpart; and a second specimen, In. 59376, from the same locality, with counterpart (Pl. 24, fig. 2).

LOCALITY. Lower Lias, Flatstones, Stonebarrow, Dorset.

PARTS KNOWN. Portion of hind wing, and ? apex of wing.

DESCRIPTION. The holotype is a fragment 34·5 mm. long, and 15 mm. wide. It thus belongs to a large species. From the preserved portions of M_4, Cu, and Cu_2 a total length of about 80 mm. can be computed. This is more than in *P. anglicana* as estimated by Tillyard. The principal new specimen is part of a hind wing, seen from the upperside. This has been ascertained from the condition of Cu_1, which is negative (depressed), whilst Cu_2 is a positive (raised) vein.

The venation leaves no doubt that this is a *Petrophlebia*, and this is confirmed by the pretty colour pattern (not mentioned by Tillyard) produced by a dusky pigmentation present along all the cross-veins.

Fragments of R and all branches of M are preserved, but of no particular interest. The area between M_4 and Cu_1 and Cu_2 is narrower towards the apex. The long middle portion of Cu_2 is remarkably straight compared with the type species and it disappears suddenly in the reticulated cross-venation, whilst in *P. anglicana* it can be traced as running in a curve down to the hind margin. The hind margin itself is not preserved.

REMARKS. This fragment (Pl. 24, fig. 1) shows, oddly enough, about the same portion of the wing as does the type species, so that a close comparison is possible. It reveals the differences mentioned; they make a specific separation necessary. The new species, *P. anglicanopsis*, is nevertheless closely related to the type species.

The holotype of *P. anglicanopsis* is partly covered by a fragment of an ammonite, probably *Asteroceras obtusum* (J. Sowerby). The marine context of sedimentation is thus evident, and the poor condition of the wing, with its corroded edge, suggests prolonged drifting.

The second specimen is tentatively referred to this species, though it shows some resemblance to *Diastommites liassina* (Strickland). It will be necessary to study the affinities of this species with care, as it may prove to be closely related to *Petrophlebia*.

Genus ***LIASSOPHLEBIA*** Tillyard (1925 : 13)

TYPE SPECIES. *Liassophlebia magnifica* Tillyard (1925 : 14).

REMARKS. Apart from the type species, Tillyard included in this genus one species first described by Hagen (1850) as *Heterophlebia westwoodi* and later (Hagen, 1866) transferred to *Tarsophlebia*. This assignation was accepted by Handlirsch; it established the relationships of the entire family subsequently erected by Tillyard.

Tillyard further described three new species. Two new species are described in the present paper, and some additional information concerning the type species is provided. There is, in addition, a fragment which cannot be assigned to a species with certainty, though it clearly belongs to the genus.

Liassophlebia magnifica Tillyard

(Pl. 27, fig. 1)

1925 *Liassophlebia magnifica* Tillyard, p. 15, pl. 1, fig. 3 ; pl. 2, fig. 4 ; text-figs. 3, 4.

MATERIAL. British Museum (Nat. Hist.), In. 64000 (Pl. 27, fig. 1), In. 59106 and In. 49213, all from The Flatstones, Stonebarrow, Charmouth, Dorset. All with counterparts.

EMENDED DESCRIPTION. Tillyard's description and illustration of the anal area of the hind wing (poorly preserved in the holotype) can be improved with the aid of In. 64000, which shows the details with unusual clarity (Pl. 27, fig. 1). Most important, there is an anal angle after all, and as sharp as in most Anisoptera, as well as a large triangular basal cell, into which a short, blindly-ending cross-vein protrudes from A. Tillyard was right in suspecting that the subquadrangle contained a group of three cross-veins, which he dotted in his text-fig. 4, except that the third, which points downwards, does not join up with another vein, but ends blindly. A similar " blind end " protrudes into the discoidal cell. The basal vein of the subquadrangle continues quite straight beyond this structure down to the posterior angle of the wing.

REMARKS. This is the only dragonfly species common to both the Charmouth and the Midlands Lias.

Liassophlebia jacksoni sp. n.

(Pl. 25)

DIAGNOSIS. Hind wing with 14 postnodals.

HOLOTYPE. British Museum (Nat. Hist.), In. 53999, with counterpart. Jackson Coll., the only specimen.

LOCALITY. Lower Lias : Flatstones, Stonebarrow, Charmouth, Dorset.

PARTS KNOWN. Hind wing only, portion beyond pterostigma not preserved.

DESCRIPTION. As for *Progonophlebia* from the Lias of Gloucestershire (Zeuner, 1958), this description and those that follow use exactly the same venational nomenclature as Tillyard (1925). It will thus be possible to compare the species and identify material. It does not, however, imply that I am in agreement with Tillyard regarding the names given to certain veins. The matter, which raises the problem of the crossing of tracheae in the immature wing, is too complicated to be discussed here and requires further studies not only of Recent material but of fossils.

Total length of hind wing about 83 mm. (computed value ; 67 mm. preserved). This compares with 70 mm. in *L. magnifica*. Greatest width, 28 mm., compared with 21 mm. in *L. magnifica*.

Pterostigma not fully preserved, basal side apparently vertical. Nodus situated nearer the base than the tip of the wing. Fourteen postnodals (only 10 in *L. magnifica*). Subquadrangle traversed by one strong vein, which is concave towards the apex.

M_{1A} weak, reduced to a short length, and joining M_2. More distad, the two veins separate again. This condition is confirmed by the counterpart specimen. Oblique vein between M_2 and M_S present and situated below the seventh postnodal. Between

M_4 and Cu_1, distad of the triangle, four rows of cells (only two in *L. magnifica*). Base of wing with straight vertical vein as in *Aeschna*. Dark pigmentation at the base in two distinct patches, one on Sc + R, the other on Cu.

REMARKS. This species is much larger than *L. magnifica* Tillyard, described from Warwickshire, and several of the venational characters are in keeping with this, as they strengthen the large wing.

The size of the wing has been computed in the following way. If the distance from the nodus to the pterostigma is used as a basis for the calculation, the total length would amount to 83·5 mm. On the other hand, if the width is used, assuming proportions similar to those of *L. magnifica*, the wing would have been 93 mm. long. This is improbable, since the preserved length between nodus and pterostigma should then be longer than it actually is and contain even more than 14 postnodals. Thirdly, assuming the proportions of both species to be the same and using the distance from nodus to pterostigma, one arrives at 78 mm. This is too short, for the postnodal section of the new species is proportionately longer than the antenodal. Thus, the most likely length is 83·5 mm., and it emerges that the new species is much broader then *L. magnifica*. If it had the same length/width ratio as this species, it should be only 25 mm. broad instead of 28 mm. as measured. It is safe, therefore, to regard the size given in the description as approximately correct. The insect must have presented a magnificent sight, with its wing-span of between 7 and 8 inches, when flying over the estuaries of Liassic Charmouth.

The difference in pigmentation, compared with the type species, confirms that the Charmouth species cannot be a large individual of the Warwickshire species.

The new species is named after Mr. J. F. Jackson of Charmouth, the indefatigable collector of Dorset fossils. *Liassophlebia jacksoni* is the seventh species of the genus to be described. The genus must have been flourishing in the British Lias, and it is curious that it has not yet been found elsewhere.

Liassophlebia gigantea sp. n.

(Pl. 27, fig. 2)

Diagnosis. Very large *Liassophlebia* with cross-vein linking Cu with arculus in fore wing so as to form a triangle.

HOLOTYPE. British Museum (Nat. Hist.), In. 51030, with counterpart. Jackson Coll., the only specimen.

LOCALITY. Lower Lias: Woodstones, Black Ven, Charmouth, Dorset.

PARTS KNOWN. Basal portion of fore wing.

DESCRIPTION. Two very strong antenodals (called "hypertrophied" by Tillyard in other species). From these and from the width between C and Cu the length of the wing can be calculated. The former index gives 82 mm., the latter 84 mm. for the fore wing. The size of this species, therefore, must have been about the same as that of *L. jacksoni*.

The arculus is continued by an exceptionally strong vein on the distal side of the discoidal cell. This vein is approximately at right angles to the long axis of the wing; in fact, it is very slightly turned back. In *L. magnifica*, it is distinctly turned forwards.

It is also distinguished by a cross vein which connects Cu with the arculus, whilst in *L. magnifica* the discoidal cell is open at the base.

From *L. withersi* Tillyard (which is a much smaller species) it is distinguished by the same characters, except that *L. withersi* also has a closed discoidal cell. The closing cross-vein is, however, much nearer to the base of the wing.

REMARKS. Though identical with *L. jacksoni* in size, this specimen has very much thicker veins. It is for this reason that it is here regarded as a distinct species.

Liassophlebia sp.

MATERIAL. British Museum (Nat. Hist.), In. 53972, with counterpart. Jackson Coll.

LOCALITY. Lower Lias: Flatstones, Stonebarrow, Charmouth, Dorset.

DESCRIPTION. A fragment of C, Sc and R of a hind wing as far as the nodus, and traces of M and Cu. Length from first antenodal to nodus, 23·5 mm.

REMARKS. The two "hypertrophied" antenodals prove that this is a *Liassophlebia*. The fragment appears to have suffered much from softening in water, for there are two unusual features difficult to explain as genuine venational elements, viz., the C is depressed between the two antenodals, and basad of the second antenodal Sc and R seems to be fused. It is inadvisable, therefore, to assign this fragment to a particular species, though it is likely to belong to one of them.

Family ARCHITEMIDAE Handlirsch

Genus ***DIASTATOMMITES*** Handlirsch (1920 : 178)

For status of family and genus, see Tillyard (1925).

Diastatommites liassina (Strickland) ?

(Pl. 27, fig. 3)

1840 *Aeshna liassina* Strickland, p. 301, fig. 11.
1856 *Diastatomma liasina* (Strickland) Giebel, p. 276.
1906 *Diastatomma liasina* (Strickland) : Handlirsch, p. 465.
1925 *Diastatommites liassina* (Strickland) : Tillyard, p. 23.

MATERIAL. One specimen, British Museum (Nat. Hist.), In. 59375, with counterpart, from the Lower Lias: Flatstones, Stonebarrow, Charmouth, Dorset. Jackson Coll.

REMARKS. I refer this small fragment to *Diastatommites* with considerable hesitation. It appears to be the anal portion of a hind wing. If so, Cu_2 is exceptionally strongly curved. It is to be hoped that more and better material will be discovered which would help also to clear up the uncertainty regarding the systematic position of this genus.

Length of the fragment, 22 mm.

Three other tiny fragments of dragonfly wings, In. 49247 (Stonebarrow), In. 53895

(Black Ven) and In. 59109 (Stonebarrow), may be mentioned to complete the record. They are unidentifiable.

Order *ORTHOPTERA SALTATORIA*

Suborder ENSIFERA

Family PROPHALANGOPSIDAE Caudell

Subfamily HAGLINAE Zeuner

Genus ***PROTOHAGLA*** nov.

DIAGNOSIS. A Prophalangopsid whose male elytra have almost straight longitudinal veins, except for CuP and 1A, which are regularly concave towards the fore margin.

TYPE SPECIES. *Protohagla langi* sp.n. (only species).

Protohagla langi sp. n.

(Plate 26)

DIAGNOSIS. Male fore wing broadest at end of basal third. Total length of fore wing about 67 mm. (61 mm. preserved). Maximum width 26 mm. Pattern of four dark cross-bands, most pronounced in the anterior portion of wing. Hind wings appear to exceed fore wings in length.

HOLOTYPE. British Museum (Nat. Hist.), In. 59018, with counterpart. Jackson Coll., the only specimen.

LOCALITY. Lower Lias: Flatstones, Stonebarrow, Charmouth, Dorset.

PARTS KNOWN. Basal two-thirds of fore wing, distal portion of hind wing.

DESCRIPTION. Fore wing very large, length about 67 mm., of which 61 mm. are preserved, maximum width 26 mm. In spite of this, the venation is slightly simpler than in other genera. Four dark cross-bands form a conspicuous colour-pattern of the fore wing. The tip of the hind wing also appears to have been darkened.

Precostal area well developed and separated from the rest of the fore margin by a conspicuous long C. The outline of the part resembles that of *Tettigonia viridissima* L. Sc extending over about five-sixths of the fore margin ; it has 14 branches.

R separated from Sc by a field of densely-spaced parallel cross-veins, area between R and Rs similar, but wider, with at least three branches, the first of which is independent as in *Hagla*. Rs with at least four, possibly five, branches.

M separated from R by an area of densely-spaced parallel cross-veins at right angles to the longitudinal veins, but between Rs and M they are oblique.

M three-branched, as in the female of *Hagla*, MA being a simple fork, whilst MP begins with a short oblique stalk, is fused with CuA for some distance, and then free again. The free portion is almost straight and undivided.

Cu consisting of a forked CuA, an unbranched Cu_n, and an unbranched CuP, as in

Hagla. It differs, however, from that of *Hagla* in that *both* Cu_n and CuP branch off before the junction with MP (in *Hagla* Cu_n distad, see Zeuner, 1939, pl. 26, figs. 2, 3). Cu_n is slightly concave towards the fore margin, CuP pronouncedly so. The areas between CuA and Cu_n, and between Cu_n and CuP, are thus broadest in the middle.

Of 1A, only the basal and distal portions are preserved. It is strongly concave towards the fore margin near the base and, if a line in the third fifth of the area between CuP and 1A is correctly interpreted as part of the latter vein, slightly bent towards the fore margin in this zone. This would give it a somewhat wavy run, though one very much less intense than in *Hagla*.

The anal area being damaged, 2A, 3A and Ax (if present) cannot be seen.

The hind wing is folded and lies beneath the fore wing. It appears to have exceeded the latter in length, for its tip is darkened. The traces of veins that can be discerned call for no comment.

Discussion and remarks. This magnificent fossil is remarkable in several respects. From the point of view of preservation it is evident that both fore and hind wing were nipped off simultaneously at the base, and the victim was not then flying. Considering how detached the movements of the wings of Saltatoria are whilst in flight, they must have been tightly closed at the time when the insect was being dismembered. This makes one think of a predator that caught it over the land, rather than of a dragonfly catching a flying insect over the water. What sort of predator this may have been is guesswork for the time being ; perhaps it was a flying reptile.

In general appearance *Protohagla* must have resembled *Tettigonia* rather than *Prophalangopsis*, or perhaps more still one of the large tropical Phaneropterinae with irregularly-veined fore wings and long hind wings, such as *Zeuneria* sp.

The affinities of *Protohagla* are with *Hagla*, a well-known genus from the British Lias. The simple venation of *Protohagla* might at first sight suggest that the specimen is a female, but the inverted run of Cu_n, CuP and 1A clearly indicates modifications in the direction of those observed in the males of *Hagla*, where the peculiar kink in these veins foreshadows the way in which the stridulating organ of the later Prophalangopsidae and Tettigoniidae was to evolve. In the females of *Hagla* these veins are unspecialized and convex towards the fore margin.

Protohagla langi is the most primitive Prophalangopsid so far known, though not the oldest, *Notopamphagopsis bolivari* Cabrera from Argentina being of Triassic age. *Protohagla* is an important phylogenetic link with the Gryllacrididae, of which *Jurassobatea gryllacroides* Zeuner from the Upper Jurassic of Solnhofen, Bavaria, shows several features reminiscent of the fore wing of *Protohagla*, especially CuP, 1A and 3A being bent in a similar manner, and the cross-venation being parallel, not reticulated. The new genus thus connects the Prophalangopsidae more closely with the Gryllacrididae, the most primitive family of all Saltatoria Ensifera.

The species is dedicated to Dr. W. D. Lang, F.R.S., who first recommended to me the insects of the British Lias as a subject worthy of study. That he was right in regarding them as such is borne out by the many descriptions that have appeared in the last thirty-five years, as well as by Mr. Jackson's discoveries at Charmouth, with which Dr. Lang is closely connected.

Order *COLEOPTERA*

Family Cupedidae

Genus ***LIASSOCUPES*** nov.

Diagnosis. Cupedid with rounded pronotum.

Type species. *Liassocupes parvus* sp. n. (only species).

Liassocupes parvus sp. n.

(Pl. 27, fig. 4)

Diagnosis. As for genus.

Holotype. British Museum (Nat. Hist.), In. 64008. Jackson Coll., the only specimen.

Locality. Lower Lias : Flatstones, Black Ven, Charmouth, Dorset.

Parts known. Elytra, pronotum, head.

Description. The specimen is a well-preserved beetle, but unfortunately the distal part of the elytra is missing. The elytra must have been about twice as long as the preserved portion.

Width of beetle across elytra, 2·6 mm., preserved length of elytra, 4·0 mm., pronotum, 1·9 mm.

The elytra show the dense regular network of longitudinal ridges with numerous cross-connections characteristic of the Cupedidae. On the assumption that this beetle had the same slender shape as Recent *Cupes*, they should have been long and parallel-sided. There are eight or nine longitudinal lines in the network, of which the fourth is distinctly stronger, another Cupedid feature. In life this fossil must have resembled the Recent *Cupes capitatus* Fabr. of North America in general appearance.

The pronotum and head lie directly in front of the elytra, tilted at an angle of 135 degrees to the right, evidence of severe water-logging. The pronotum is almost circular and shows no spines or other details. It is narrower than the pair of elytra, and this is again another Cupedid characteristic.

The head is poorly preserved, but its granular surface is discernible, the mandibles can be recognized and the head is inserted horizontally in front of the pronotum. No spines or protuberances can be seen, and the antennae are not preserved.

Remarks. The shape of the pronotum and the exceptionally small size are characteristic. Its sculpture distinguishes this species from the fragment recently described by Gardiner (1961 : 87) as *Metacupes harrisi*, from the Rhaetic of Bridgend, Glamorgan.

Family ?

Genus ***HOLCOËLYTRUM*** Handlirsch (1906 : 453)

Diagnosis. Beetles with elytra with conspicuous black and white longitudinal stripes.

Type species. *Holcoëlytrum giebeli* Handlirsch, 1906, by monotypy.

DISTRIBUTION. Lower Lias of England.

REMARKS. The two species described by Handlirsch as *Holoëlytrum giebeli* and *Holcoptera schlotheimi* are unlikely to belong to different genera. The holotypes of both are reported to have been incorporated in the British Museum, but only that of the first species is known. It is unwise, therefore, to use the second as the type species. The holotype of *Holcoëlytrum giebeli*, though only a fragment of an elytrum, is recognizable, so that this species defines the genus satisfactorily. It is, incidentally, by far the more common species. For lack of generic differences, *Holcoptera* is therefore here regarded as a synonym of *Holcoëlytrum*, which genus now contains the two species easily distinguishable as follows:

(1) Elytrum about 12 mm. long, with 5 black stripes . . *Holcoëlytrum giebeli* Hdl.
(2) Elytrum about 5 mm. long, with 4 black stripes . . *Holcoëlytrum schlotheimi* (Hdl.)

Holcoëlytrum giebeli Handlirsch

(Pl. 27, figs. 6–8)

1845 (Harpalideous Carabidae) Brodie, pp. 101, 124, pl. 10, fig. 2.
1856 *Harpalus Schlotheimi* Giebel, p. 63. (*Partim.*)
1906 *Holcoëlytrum Giebeli* Handlirsch, p. 453, pl. 41, fig. 64.

DIAGNOSIS. Elytrum over 10 mm. long, with five black stripes.

DISTRIBUTION. Lower Lias of England.

HOLOTYPE. British Museum (Nat. Hist.), I. 3581. Brodie Coll. Probably from Apperley, Gloucestershire.

MATERIAL. In addition to the holotype, forty-three specimens from the Flatstones of the Lower Lias of Charmouth, Jackson Coll., as follows:

(a) *Stonebarrow, Charmouth, Dorset*

Bodies with both elytra, with counterpart: In. 51002 (Pl. 27, figs. 7, 8), 53928, 53937; three specimens.

Single elytra, with counterpart: In. 49204, 43981, 49563, 49229, 49570, 49227, 49611, 49228, 53989, 53962, 49239, 53985, 49585, 59129, 59141, 59134, 59153, 59117, 64013, 64012, 59145, 49244, 64009; twenty-three specimens.

Single elytra without counterpart: In. 64010, 64011, 49149, 53943, 49219, 53974, 49610, 49616 (Pl. 27, fig. 6), 59148, 59138; ten specimens.

(b) *Black Ven, Charmouth, Dorset*

Single elytra with counterpart: In. 49209, 59100, 48163, 49621; four specimens.

Single elytra without counterpart: In. 49619, 49211, 59393; three specimens.

Total, forty-three specimens.

PARTS KNOWN. Elytra, scutellum, tip of abdomen (In. 53928), fragment of leg (In. 53937).

DESCRIPTION. No complete beetles have so far been found. The three specimens with pairs of elytra look broader and stouter than they would have appeared in life, since they are dorsoventrally compressed, causing the elytra to gape at the distal end. Size and shape are comparable with a large *Tenebrio molitor* L., or with *Feronia* sp. The scutellum is very small, and the fragments of abdomen and leg present no features worth mention. In. 51002 shows the underside of the body (on the counterpart), in addition to the striped elytra (Pl. 27, fig. 8).

The elytra are noteworthy for their longitudinal stripes. In the diagnosis they have been given as black. Alternatively, the unpigmented interstices can be counted. There are at first sight four of them. The outer (anterior) margin of the elytron also is represented by a pale line (In. 49616). Counting this as Line 1, one finds that Nos. 1 and 2 are joined near the apex, continuing as a single line for a short distance and ending free within the black. Also, Nos. 3 and 5 are similarly joined, without continuation. They thus enclose No. 4. All are bent towards the shoulder near the base and towards the apex at the distal end. It is evident that these lines represent the veins, whilst the black lines are the interstices. The veins represented are Sc (Line 1), R, Rs, M, and Cu, on the interpretation given to the elytral ridges of the Cupedidae by Zeuner (1933 : 294).

The question arises whether the veins were ridges in the elytra. They could equally well have been immersed within the elytron. A break between the upper and the lower cuticles would result in the same structure on the rock surface as would be produced by ridges.

Some specimens show only three black stripes, the inner and the outer being absent. In these cases, the white lines are broader than usual. One may be inclined to regard these as a different species, but In. 53981 demonstrates conclusively that both variants are merely aspects of the same type of elytron. In the specimen mentioned part and counterpart have five and three black stripes respectively. Unfortunately, this specimen is much flattened. On the counterpart, the anterior edge is distinctly bent upwards, as it is in a large number of Recent beetles. It may thus be presumed that the three-striped aspect is the lower (or underside) of the elytron. This is confirmed by one of the few specimens that have retained some of their original curvature. In specimen In. 49611 the surface is distinctly convex, identifying this as a left elytron. Its colourless lines are very distinct on the counterpart, which is the negative of the upper surface. Since they are wider on the lower part, they must represent lumina in the elytron. It is highly probable, therefore, that these elytra had five ridges corresponding to the major longitudinal veins, and that the membrane between the veins was pigmented black.

One further detail is supplied by In. 49616, and less clearly by others. There is a concentration of black along the white lines, whilst the central portions of the dark stripes are grey. It appears that the latter were thinner than the sides of the ridges. This is as it should be if the ridges contained tracheal lumina.

Having ascertained the structure of the elytron, it is now possible to describe it in some detail.

Elytra 11·8–13·5 mm. long, and up to 4·0 mm. wide (less originally, since flattened *post mortem* ; 3·5 mm. normal). Black, with four prominent ridges corresponding to R, Rs, M, Cu. These and the anterior edge (Sc) usually colourless in the fossils which are split between the upper and lower membranes. Sc and R joined distad, with a short single continuation, Rs and Cu likewise joined distad but not continued. M inside the area enclosed by Rs and Cu, without touching them. On specimens showing the veins as white lines, shoulder portion always black. All veins, except Sc, bent forwards at the base.

REMARKS. Brodie (1845 : 124) regarded this species as " appearing in form nearest to the Harpalideous Carabidae ". Handlirsch refuted this, and its systematic position must remain uncertain until a specimen with head and pronotum is found.

Nevertheless, owing to the five " black stripes " separated by four " white lines ", the species is the most easily recognized among the beetles of the British Lias.

Holcoëlytrum schlotheimi (Giebel)

(Pl. 27, fig. 5)

1845 (Harpalideous Carabidae) Brodie, pp. 101, 124, pl. 6, fig. 28.
1856 *Harpalus Schlotheimi* Giebel, p. 63.
1906 *Holcoptera Schlotheimi* Giebel : Handlirsch, p. 453, pl. 41, fig. 63.

DIAGNOSIS. Elytron over 5 mm. long, with four black stripes.

DISTRIBUTION. Lower Lias of England.

HOLOTYPE. British Museum (Nat. Hist.), I. 3582. Brodie Coll., from Binton, Warwickshire, is supposed to be the holotype. The specimen is labelled as " Carabidae (Harpalideous), Figd. Brodie, Foss. Ins. pl. 6, f. 28, p. 101, 124, Brodie Coll." Except in size, however, it does not agree with the figure referred to, being uniformly black and lacking the stripes. The specimen is marked on the rock itself " Binton ", and on a label glued to it is written " Carabidae Pl. 6, f. 28 " and on the reverse " Harpalideous Carabidae ". This appears to be in Brodie's own handwriting, so that the mistake was made by Brodie himself. The locality given in his book (p. 101) is Apperley or Brockeridge. Since Apperley is the type locality of *H. giebeli*, the type of *H. schlotheimi* should have come from Brockeridge.

It is clear, therefore, that the specimen marked as the type, I. 3582, is not the holotype, and that the true holotype was lost long ago, probably in Brodie's time. For diagnostic characters one has to rely on Brodie's illustration and description, and a Neotype has been selected from the new material.

NEOTYPE. British Museum (Nat. Hist.), In. 59115, from the Flatstones, Stonebarrow, Charmouth, Dorset. Jackson Coll. (Pl. 27, fig. 5).

OTHER MATERIAL. In. 53990 with counterpart, from the same locality.

PARTS KNOWN. Elytra in pairs, parts of prothorax.

DESCRIPTION. Of the two specimens available, In. 59115 shows the same kind of black stripes as *H. giebeli*. There are two in the central part of the elytron, and one thin one along the hind margin. The latter touches the corresponding stripe of the other elytron in the position of rest, so that the beetle appears to have five stripes. The intervening white lines are broader in this species than in *H. giebeli*, and all join the pale anterior margin at the apex. Their bases are bent forward as in the other species. One vein, therefore, is not marked (or atrophied) in *H. schlotheimi*. Most probably R lies close to Sc, the black stripe between them being missing.

The dorsal counterpart of the second specimen (In. 53990) is almost uniformly black, confirming the observations made on the extensive material of *H. giebeli*; but in this specimen the longitudinal ridges are discernible, and there appears to be a fine punctation present on the surface of the elytron

The scutellum and a portion of the prothorax are preserved in In. 53990, without providing diagnostic information.

Elytra 5·5 mm. long, 3 mm. wide.

REMARKS. This species is much rarer than *H. giebeli*. There can be no doubt that the two specimens described here belong to *H. schlotheimi*, based on Brodie's figure (1845, pl. 6, fig. 28).

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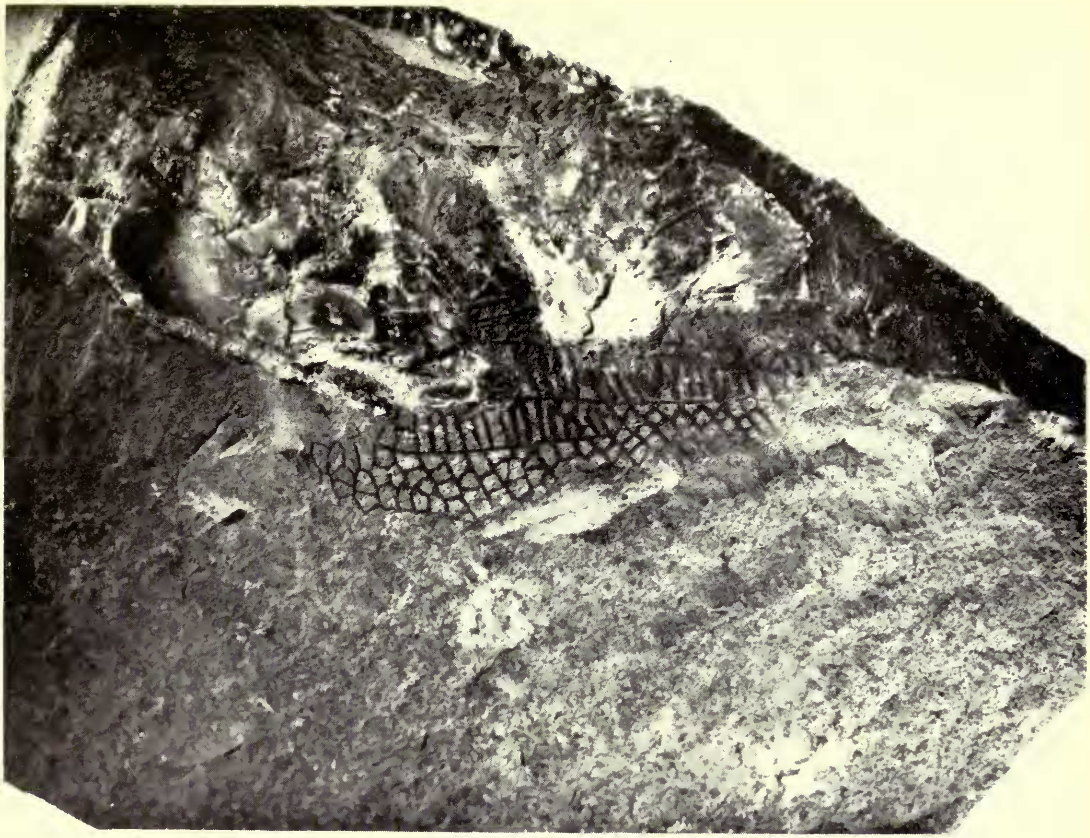
PLATE 24

FIG. 1. *Petrophlebia anglicanopsis* sp. n. Holotype. In. 49573. ×1·85.
FIG. 2. A second specimen doubtfully referred to *P. anglicanopsis*. In. 59376. ×2·2.



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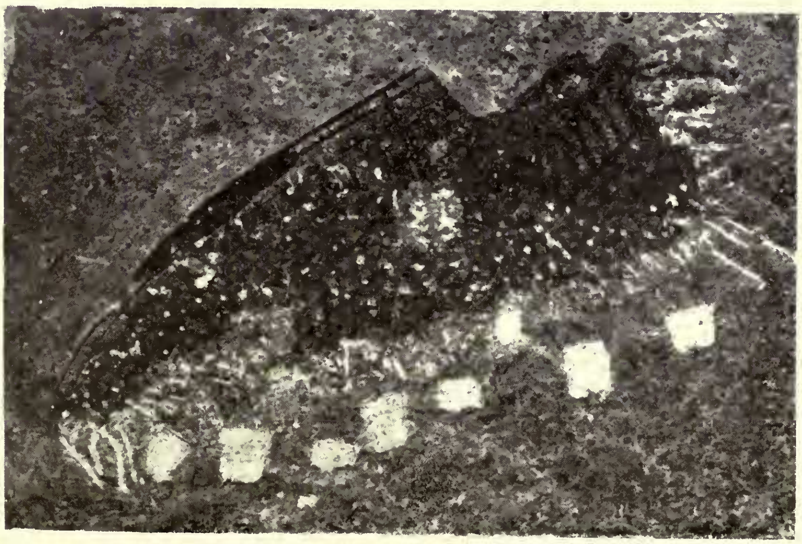
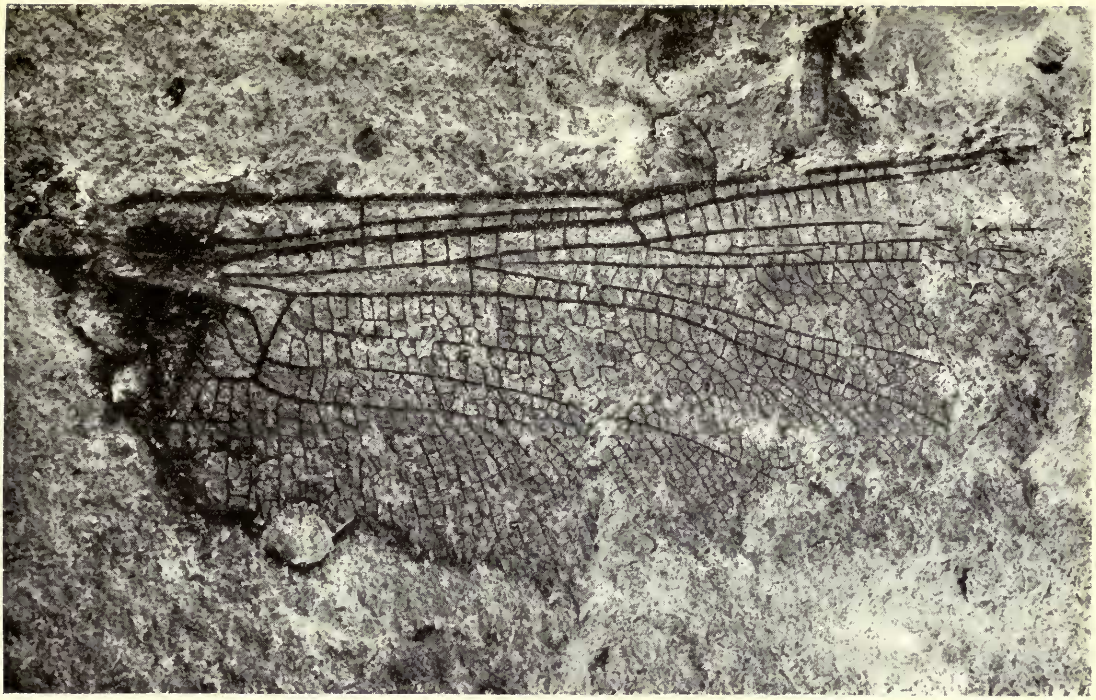


2

PLATE 25

Figs. 1, 2. *Liassophlebia jacksoni* sp. n. Holotype (Fig. 1) and counterpart (Fig. 2). In. 53999. ×2.



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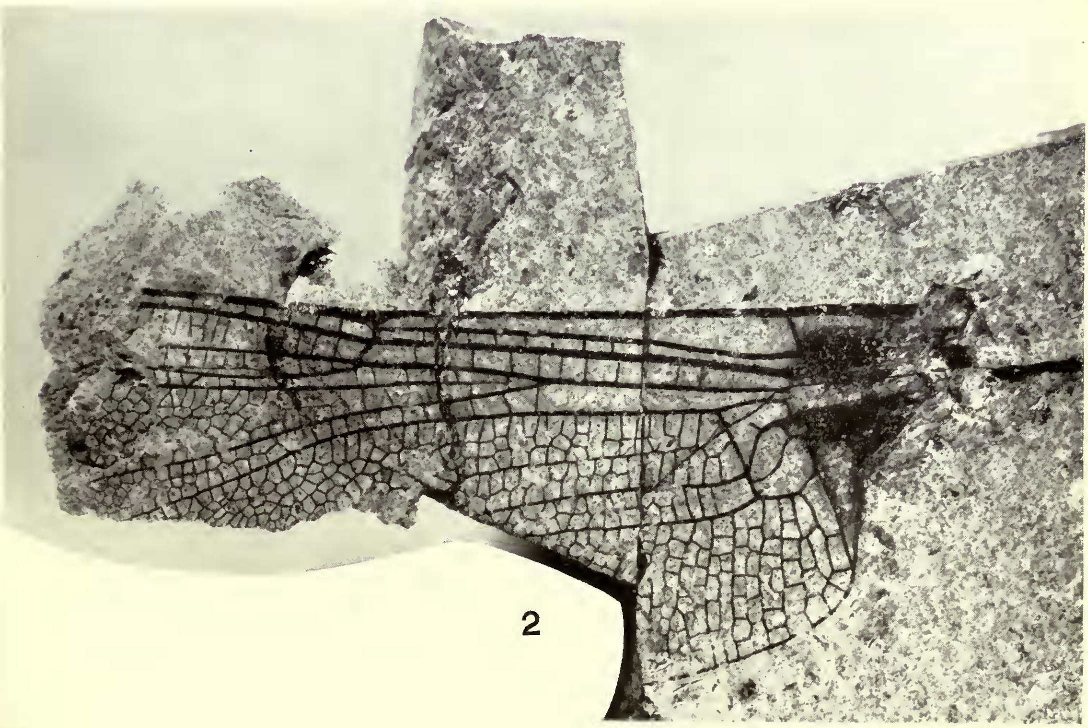

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PLATE 26

FIGS. 1, 2. *Protohagla langi* gen. et sp. n. Holotype (Fig. 1) and counterpart (Fig. 2). In. 59018. × 1·7 and 1·6 respectively.

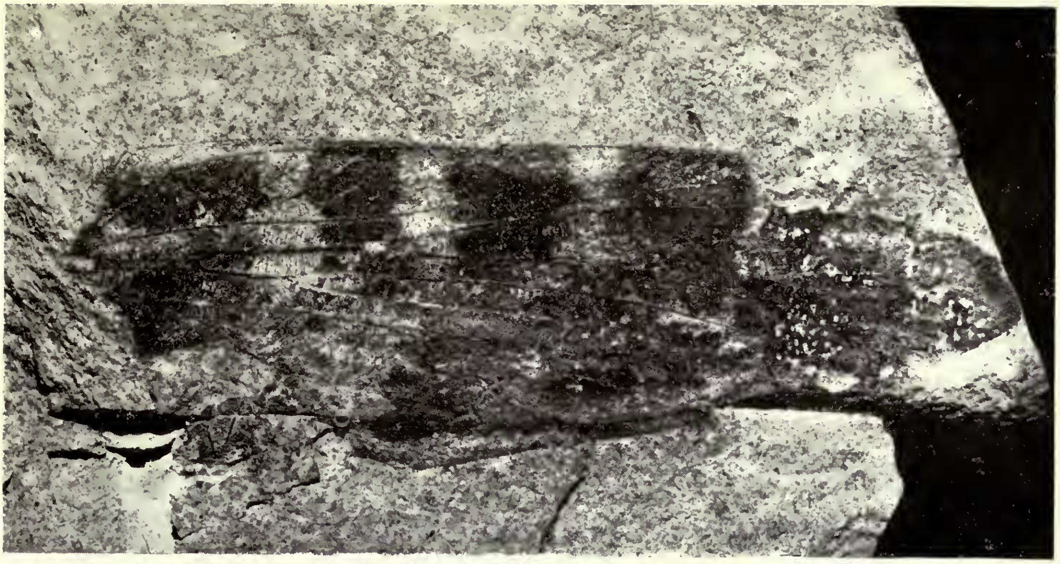

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PLATE 27

FIG. 1. *Liassophlebia magnifica* Tillyaid. In. 64000. ×2·4.

FIG. 2. *Liassophlebia gigantea* sp. n. Holotype. In. 51030. ×2.

FIG. 3. *Diastatommites liassina* (Strickland) ? In. 59375. ×2.

FIG. 4. *Liassocupes parvus* gen. et sp. n. Holotype. In. 64008. ×10. On the right above the pair of elytra lie the pronotum and head, cut off in this print.

FIG. 5. *Holcoëlytrum schlotheimi* (Giebel). Neotype. In. 59115. ×2·9.

FIG. 6.—*Holcoëlytrum giebeli* Handlirsch. In. 49616. ×3·1.

FIG. 7. *Holcoëlytrum giebeli* Handlirsch. A pair of elytra. In. 51002. ×2·9.

FIG. 8. *Holcoëlytrum giebeli* Handlirsch. Underside of specimen shown in Fig. 7. ×2·9.

1

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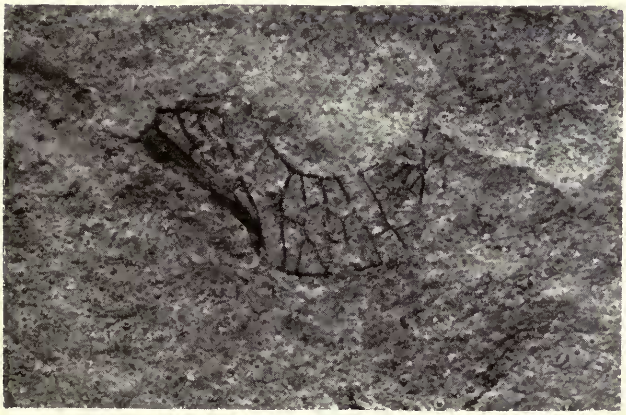

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